

SIZE-FREQUENCY AND GROWTH-RING ANALYSES OF *MYTILUS EDULIS* AND *CARDIUM EDULE*, AND THEIR PALAEOECOLOGICAL SIGNIFICANCE

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ABSTRACT. The population growth patterns of living *Mytilus edulis* and *Cardium edule* from the Firth of Forth, Scotland, are analysed. Fossil communities and death assemblages derived from the living populations are also investigated and the size-frequency patterns of living and dead shells compared. The use of growth-ring analysis as a tool in palaeoecology is considered.

Size-frequency criteria used in the discrimination of fossil communities and death assemblages are critically re-examined. It is argued that mortality rates among preservable young in many cases may be much lower than has hitherto been assumed. Symmetrical size-frequency distributions in fossil species, therefore, need not necessarily indicate size sorting. A distinction is drawn between age-mortality rates derived from living animals and size-mortality rates determined from fossils.

PALAEONTOLOGISTS are necessarily dependent for interpretation of their subject-matter on a thorough knowledge of living organisms, yet those working in the field of palaeoecology are frequently faced with problems that have not aroused great curiosity among biologists and for which, in consequence, there is a dearth of relevant information. In particular, certain predictions have been made by palaeontologists about the probable character and significance of size-frequency distributions of living and dead invertebrate assemblages, which need to be tested by reference to modern forms. Furthermore, growth-rings of invertebrate shells, which are potentially very useful to the palaeoecologist, have not been the subject of intensive research by zoologists.

The work described in this paper is intended as a contribution towards these ends. We have confined our attention to assemblages of two of the commonest lamellibranchs living on the southern shores of the Forth Estuary near Aberlady, *Mytilus edulis* and *Cardium edule*, which are highly favourable for our purposes. Mussels occur crowded together in immense numbers on rock ledges on the lower part of the shore. They form an ideal community and are easy to collect. On the other hand, they lack clearly defined seasonal growth-rings and so this aspect of our work has been restricted to cockles, in which growth-rings are very pronounced. Cockles are common burrowers in the beaches and mud flats, and can be easily collected by sieving.

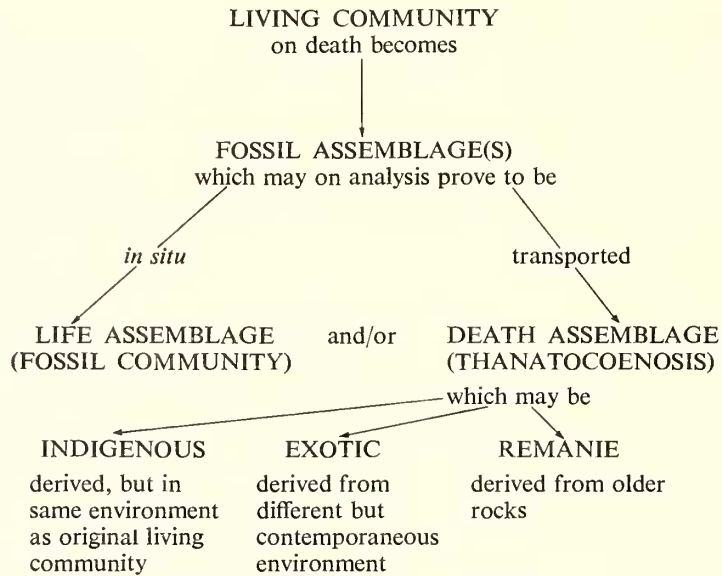
In so far as our study is strictly circumscribed, the generalizations we propose must of necessity be regarded as tentative, but we think that our approach to certain problems important in palaeoecology is in some respects new.

TERMINOLOGY

It is difficult to find satisfactory terms to describe the different animal populations which appear during the sequence of changes from the living to the dead. Palaeoecologists use one set of terms for dead organisms, ecologists another for living organisms, and only on the boundary between the two disciplines do difficulties arise. Johnson (1960)

encountered the problem in his analysis of the mode of formation of fossil assemblages. His solution was simple: life assemblage referred to living organisms, death assemblage to dead organisms or parts thereof. But these terms are commonly used in quite a different sense in palaeontology. Life assemblages as defined by Boucot (1953) refer to *in situ* fossils and death assemblages to transported fossils.

On separate occasions (Craig 1953, Hallam 1960), we have defined terms for different fossil associations and we hope that the following amalgam of our views, presented schematically below, may prove generally acceptable.



In this paper we are concerned with living communities which are in the process of transition to fossil communities and death assemblages. It is admittedly stretching definition to describe as fossils, organisms which have been dead for only a matter of months or at most a few years, but we believe this to be a justifiable extension of the normal meaning of the word. The death assemblages with which we have been concerned consist almost entirely of disarticulated valves. Hence we have found it appropriate to call these valve assemblages.

MYTILUS EDULIS COMMUNITY AT FERNY NESS

Description. The aim of this exercise was to investigate the changes in population structure in a mussel community at a selected locality from April 1961 to November of the following year. The locality chosen was a few square yards of a thickly populated mussel bank, just above mean low-tide level at Ferny Ness, at the southern end of Gosford Bay, East Lothian, Scotland. Samples were taken on four different days spaced out at approximately half-yearly intervals. The antero-posterior shell lengths of the living forms were measured in millimetres using a caliper gauge and plotted as size-frequency histograms.

Minor variations were eliminated by taking the means of adjacent millimetre measurements and replotting (text-fig. 1). This modification, which has been adopted throughout, helps to render with greater clarity the major features of the sample structure.

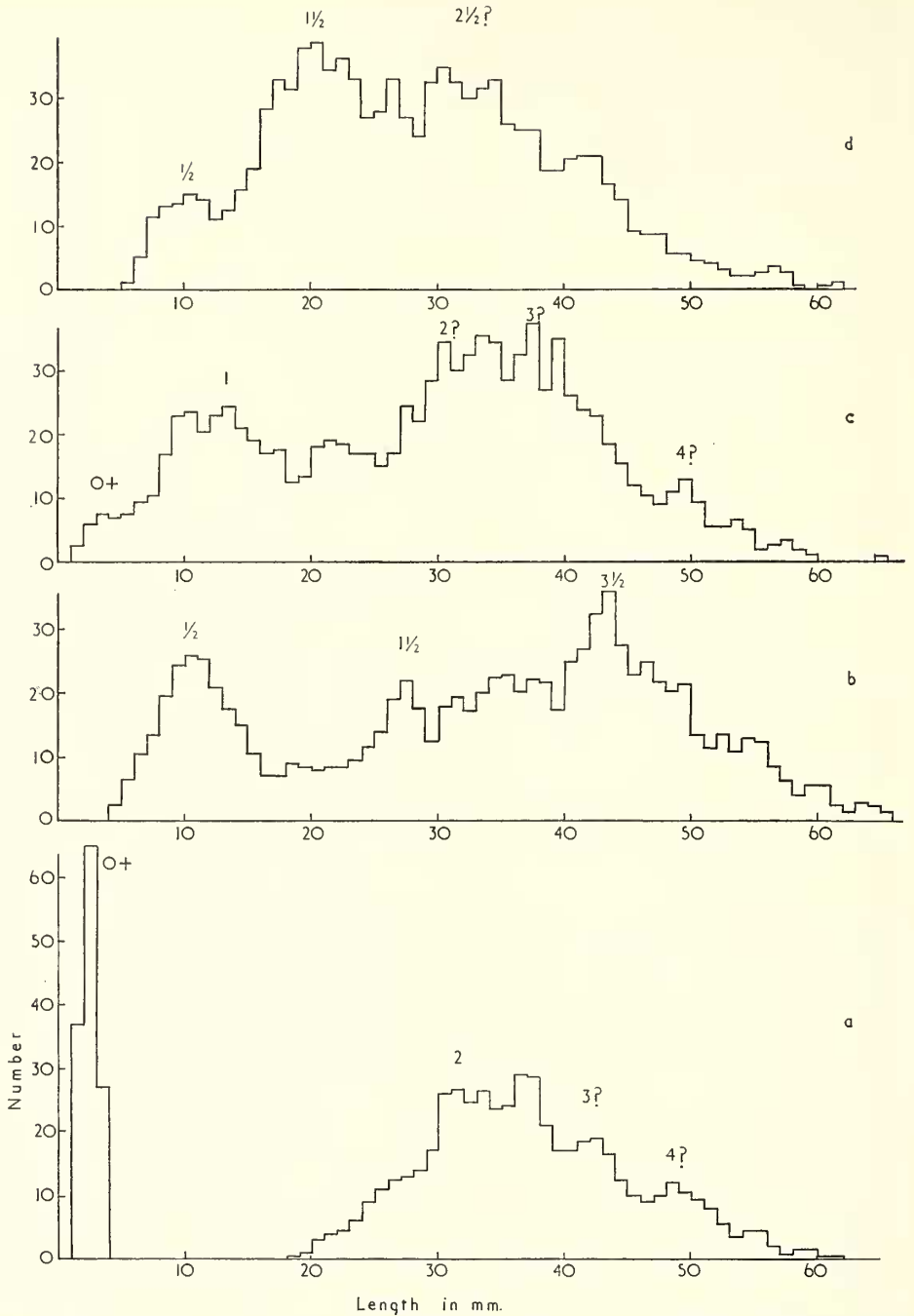
The first sample, for April 1961 (text-fig. 1*a*), was taken shortly after a heavy spatfall, which accounts for the clearly defined peak of minute individuals at the left of the histogram. The rest of the sample consists of older mussels forming a broad and fairly symmetrical cluster with minor peaks at 32 and 37 mm. In the November 1961 sample (text-fig. 1*b*) there are still two clearly defined groups, one with a low peak at 10.5 mm., more dispersed than that of the forms newly settled in April, and the other with a peak at 43.5 mm. The main change in the April 1962 sample (text-fig. 1*c*) is the overall reduction in size of the larger forms, which lack a well-defined peak. The mode of the smaller specimens has shifted to 13.5 mm. By November 1962 the two groups are no longer clearly separate, though there are notable maxima at 20.5 and 30–35 mm.; a further small peak at 10.5 mm. is distinguishable.

Interpretation. The most obvious change in the samples relates to the growth of the mussels settled in the spring of 1961, which form a distinct group whose growth can be followed throughout, with the amount of dispersion increasing with size, until, in November 1962, it has almost caught up with the older mussels. Another notable change is the overall decrease in size of the latter group between November 1961 and April 1962. Since there is no question of the size of the individuals decreasing, and, assuming the sample is at least reasonably representative of the local population, this must be due to selective mortality and removal from the population of larger (and presumably older) forms which failed to survive the winter.

A further point is that the small, but clearly defined, 10–11 mm. peak of the November 1962 sample must largely represent mussels in their first year of growth, following a late spring or early summer settlement, since there was little trace of this spatfall in April anywhere on the mussel bank.

In order to deduce more from the histograms we need further information on the growth of mussels. By far the most complete study in the British area seems to be that of Savage (1956), who closely followed mussel growth in the Conway Estuary for several years after an exceptionally heavy spatfall in the spring of 1940. A particularly valuable feature of Savage's work was his collection and length measurement at monthly intervals, from April 1940 to November 1942, of samples of 500 specimens of this age group. As plotted in terms of size frequency, the samples tend to exhibit normal or slightly positively skewed distributions, but the smallest specimens had leptokurtic or sharply peaked distributions, with the degree of kurtosis diminishing rapidly with growth until stability of distribution was substantially attained at a length mean of about 13 mm. These characteristics are the simple consequence of the degree of dispersion being proportional to the absolute value of the variate in question, namely length (Simpson and Roe 1939).

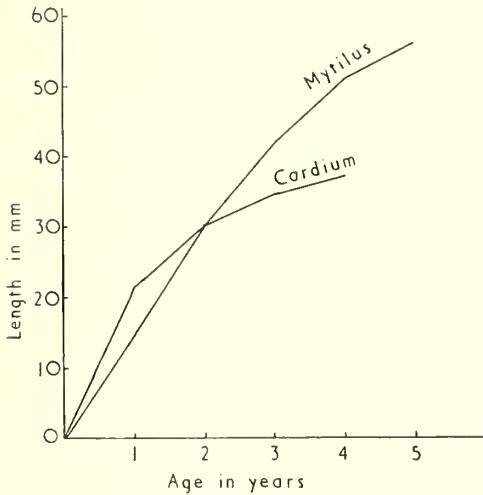
Savage also plotted growth curves for different environments from his data. These curves, one of which is illustrated in text-fig. 2, are slightly convex upward due to a gradual diminishing of growth rate with age, and are irregular in detail because of seasonal variations in growth rate (high in summer, low in winter). By combining information from the growth curve for the banks (the environment corresponding most



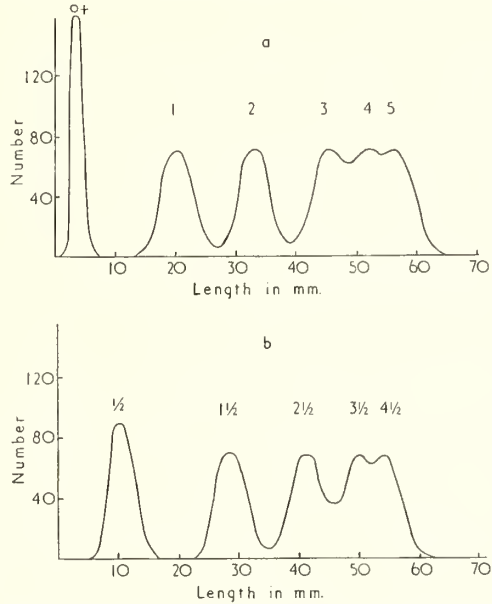
TEXT-FIG. 1. Size-frequency histograms of live *Mytilus edulis* from Ferny Ness, East Lothian. *a*, April 1961. *b*, November 1961. *c*, April 1962. *d*, November 1962.

closely with that of the Ferny Ness samples) with that from the size distributions of mussels of different ages, it is possible to construct a rough model of population structure at different seasons for five years of growth (text-fig. 3). These models assume population stability with constant annual recruitment and zero mortality, and are to this extent artificial. They can nevertheless prove most illuminating as a guide to interpretation.

Before using the models for interpretation of the Ferny Ness samples, it is necessary to compare, where possible, the rates of growth of Savage's and our specimens. This can



TEXT-FIG. 2. Graph of age plotted against length in *Mytilus edulis* and *Cardium edule*. Data taken from Savage (1956) and Orton (1926). Seasonal fluctuations in growth have been ignored.



TEXT-FIG. 3. Theoretical population models for five years of growth of *Mytilus edulis* derived from Savage's data (1956). *a*, End of May. *b*, End of October.

be done satisfactorily only for the younger forms, which cluster in clearly defined groups. The Conway specimens grew to a mean length of 10 mm. after half a year, 20 mm. after a year, and 28 mm. after one and a half years, while the corresponding figures for the 1961 spatfall at Ferny Ness are 10 mm. (also the 1962 spatfall), 13 mm., and 20 mm. Clearly, the growth rate of the Ferny Ness specimens declined somewhat after the first six months or so compared with those from the Conway.

Examining the April 1961 Ferny Ness histogram, it becomes apparent that there is virtually nothing that could be attributed to a first year age group. This is most probably the combined result of inadequate sampling and a poor settlement of spat the previous year, since the November 1961 histogram has a small, but clearly defined, peak at 28 mm., which corresponds exactly with that for one and a half years of growth in the population model for autumn (text-fig. 3*b*). Older age groups are difficult to distinguish and the age assignments in text-fig. 1 are more or less tentative.

Another notable feature of the histograms is the marked falling off in numbers of the

larger forms compared with the models. This must be the consequence of a relatively high mortality of older mussels, a point we have already noted when comparing the samples for November 1961 and April 1962. The comparatively slight mortality of the younger mussels can be illustrated, in a rough quantitative way, if attention is confined to the group settled in the spring of 1961. Assuming an approximately normal distribution of size for this group, it forms some 22 per cent. of the sample for April 1961, 36 per cent. of that for November 1961, 37 per cent. for April 1962, and 45 per cent. for November 1962. Even allowing for the vagaries of sampling, this indicates an appreciable decline in the relative abundance of older mussels as a result of death. The high loss of large specimens between the autumn of 1961 and the spring of 1962 suggests a lesser resistance of the older members of the population to winter conditions. Another important factor in their decline might have been the competition for food. An extreme case of this was cited by Savage, who commented that the intense spatfall in the Conway Estuary in 1940 resulted in the catastrophic killing of the parent population.

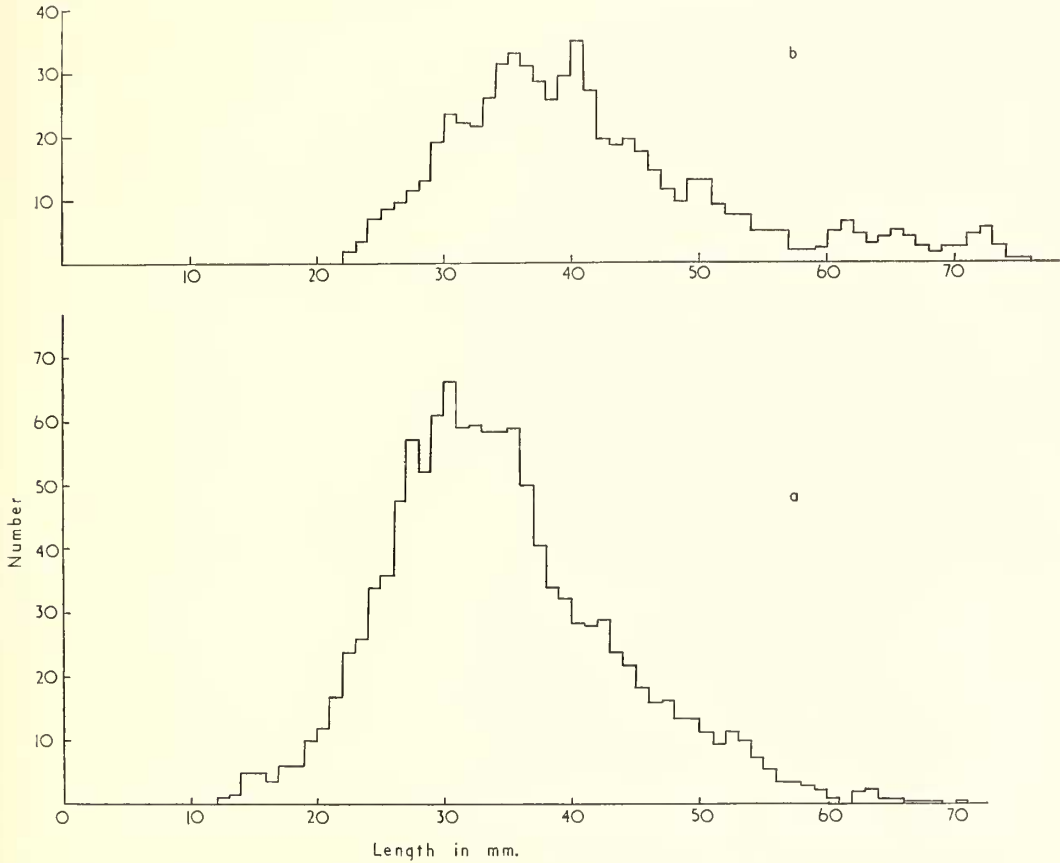
The age groups of the Ferny Ness mussels exhibit somewhat greater variability in size than those studied by Savage. This could to some extent be the result of spat settling over a greater length of time, but may largely reflect local environmental conditions. Furthermore, fluctuations in rates and times of settlement, growth and mortality all tend to blur the distinctions between age groups so apparent in the models.

The two population models may also be used for more general observations on lamellibranchs, and probably many other benthonic invertebrates in which there is seasonal growth variation and a spatfall restricted to a few months in the year. The models indicate that after the first two years or so the age groups begin to merge, a consequence, it may be observed, of a progressive slowing down of growth rather than increased size dispersion. However long the organisms live, therefore, there are never likely to be more than three clearly separated size-frequency peaks at any season. This number is likely to be a maximum, since the rate of growth of the Conway mussels seems to be somewhat atypical of lamellibranchs in general (Vogel 1959, Kristensen 1959). *Cardium edule* may be more normal in possessing a higher initial growth-rate, giving a more convex growth curve (text-fig. 2) and it is noteworthy that Orton (1926), who followed the growth of marked cockles, found that the newly settled forms caught up in size with the old after only two years of growth. Other factors tending to reduce the number of clearly defined peaks in a given population are low rates of settlement in certain years and increasing rate of mortality with age, while samples collected in the winter months will not include the newly settled young, which will give a very sharp peak.

MYTILUS VALVE ASSEMBLAGES

Description. Two samples of shell thanatocoenoses were collected for study, one from the storm beach at Ferny Ness, a short distance from the mussel banks, the other from the storm beach in Craigelaw Bay, also close to mussel banks. Both samples, though dominated by mussels, contained a mixture of shells of both sand- and rock-living organisms. The mussel shells showed almost 100 per cent. disarticulation and 50 per cent. fragmentation (by weight). The fragments have mostly been derived from larger valves, so that if there is any bias in the sample of complete valves it is towards smaller specimens. Right and left valves, often with very worn surfaces, occurred in approxi-

mately equal quantities and similar size distributions when plotted as length-frequency histograms. For this reason, only the results for the left valves are reproduced here (text-fig. 4). The two histograms are of similar form. Both exhibit a marked positive skew and would plot as comparatively smooth curves. There is a conspicuous lack of small specimens, but a small minority of valves is larger than anything found in the Ferny Ness communities.



TEXT-FIG. 4. Size-frequency histograms of *Mytilus edulis* valve assemblages from storm beaches. *a*, Ferny Ness. *b*, Craigelaw Bay.

Interpretation. It might at first be thought that the absence of small valves is the consequence of selective removal by tidal currents. That this is not the case is indicated by the associated presence of numerous small shells of other organisms, including miliolid foraminifers, barnacles and small periwinkles. That the histograms in fact express mortality is suggested by a comparison of the size distributions of the community and valve assemblage in the region of Ferny Ness. The former suggests relatively low mortality during youth, followed by relatively high mortality in the 30 to 45 mm. range. Assuming this pattern has approximately held true in this locality for a number of years, the size distribution of the neighbouring valve assemblage is very satisfactorily accounted for by

the removal and disarticulation after death of mussels on the banks by tidal currents, and their transport on to the storm beach by breakers and storm waves, without the significant intervention of size sorting.

Further interpretation must await the discussion below of mortality rates and survivorship curves.

POPULATION AND GROWTH-RING ANALYSIS OF *CARDIUM EDULE*

The common cockle, *Cardium edule*, is an abundant member of the infauna on the sand and silt beaches of the East Lothian coast. The animals are easy to collect and their shells show well-marked growth-rings. It, therefore, seemed an ideal species for the kind of population and growth-ring study that we envisaged.

Previous studies on the growth-rate of *Cardium edule* have been carried out by Orton (1926). The animals grew in a perforated metal box planted in an estuary. The shells were measured at regular intervals and marked, and in this way the rate of growth could be accurately determined. Annual winter rings were formed on the shells, as were also rings formed when the animals were disturbed. Such disturbance rings occur under natural conditions and are difficult to distinguish from annual rings.

The yearly size-ranges of the cockles in Orton's experiments were:

<i>No. of winter ring</i>	<i>Length of rings (mm.)</i>
1	19-22
2	28-32
3	33-36
4	35-39

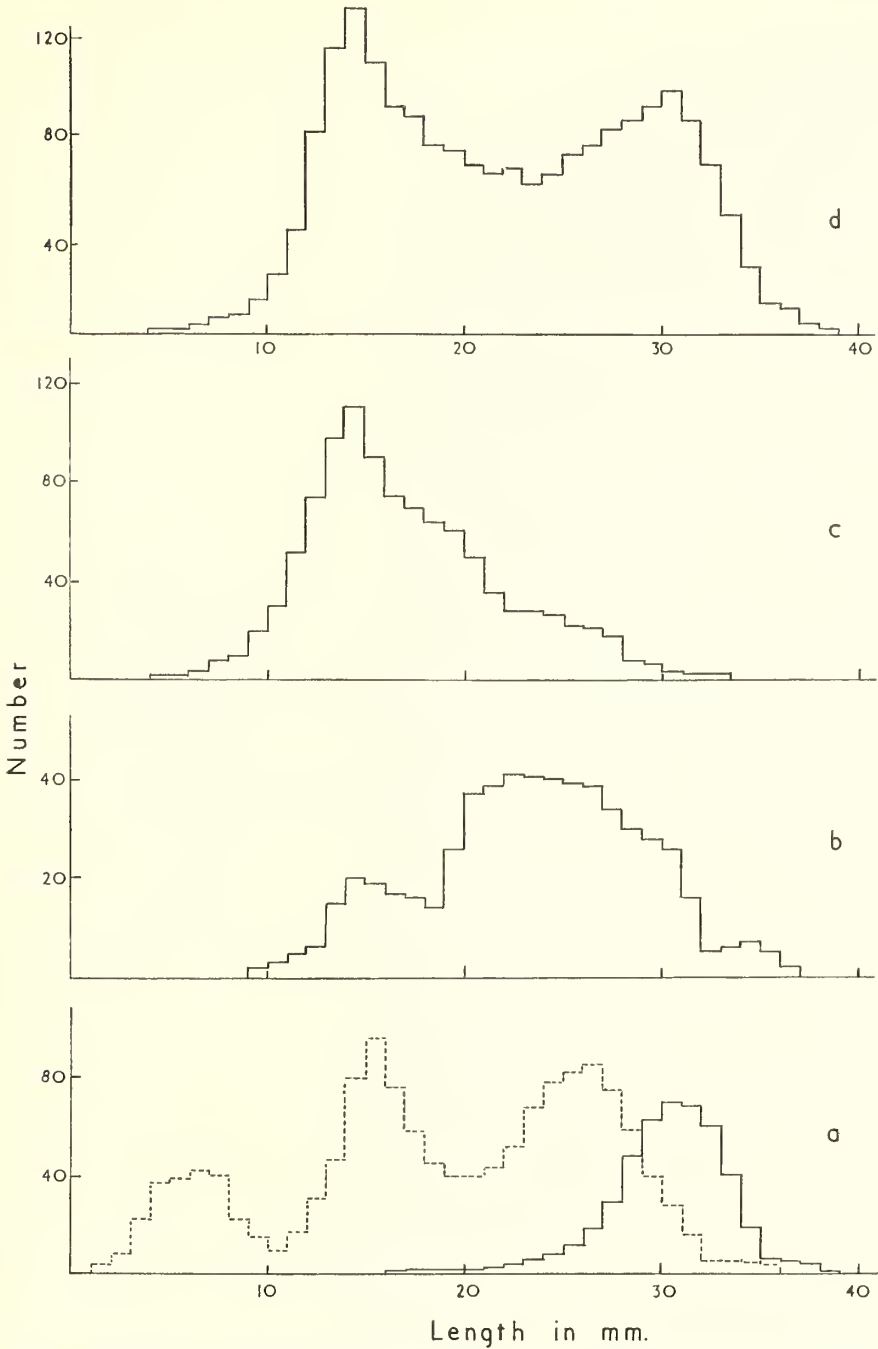
Two localities at Aberlady were chosen for collecting our samples: the first is a sand flat in Craigelaw Bay, and the second the east bank of the tidal Peffer Burn at Kilspindie. The flat is uncovered for most of the tidal flow, whereas the river bank is mostly under water. Although the river locality is the more sheltered, it has the more variable salinity.

Sediment and shells dug from an area of some 4 square yards were sieved through a 10-mesh-to-1-inch screen, and a check was made for microshells by using a 30-mesh screen. The antero-posterior length of each shell or valve, and in selected samples each visible growth-ring, was measured.

Like Orton, we frequently found it impossible to distinguish winter rings from disturbance rings and decided that the most objective method of determining the winter rings was to measure all visible growth-rings and then plot their size-frequency distribution. The resulting histograms, therefore, show the sizes of the modal growth-rings in the sample.

Description and interpretation of the Peffer sample. Some 2,900 living animals, dead shells, and disarticulated valves were sieved from one sample taken from the sediment on the east bank of the Peffer Burn in May 1962. Size-frequency histograms were constructed for the living population and their growth-lines (text-fig. 5*a*), articulated dead shells (text-fig. 5*b*), and valves (text-fig. 5*c*).

The living animals (16 per cent. of sample) form a nearly symmetrical histogram, and



TEXT-FIG. 5. Size-frequency histograms of *Cardium edule* from Peffer Burn, East Lothian, May 1962. Broken lines represent growth-ring size-frequencies. *a*, Living animals. *b*, Dead shells. *c*, Right valves. *d*, Total shells and valves.

belong substantially to one generation, which, from growth-ring analysis and earlier observations, can be shown to be the spatfall of summer 1960. There appears to have been no settlement of spatfall at the site in 1961, although we found cockle spat that year less than a mile away at Craigelaw Bay. The histogram of the growth-rings on the shells of the living animals clearly delineates the winter rings of 1960 and 1961. The early growth-ring at 6.5 mm. is similar to that found on the shells of the living cockles in Craigelaw Bay, and, in both cases, seems to have developed shortly after the spat had settled on the shore. The comparative lowness of this 6.5 mm. peak is due to the difficulty of seeing and measuring growth-rings in the abraded umbonal region.

This single 1960 generation, practically unaccompanied by the complication of other year classes, was ideal for our purpose, because the simple population structure could be easily traced from the living to the fossil state.

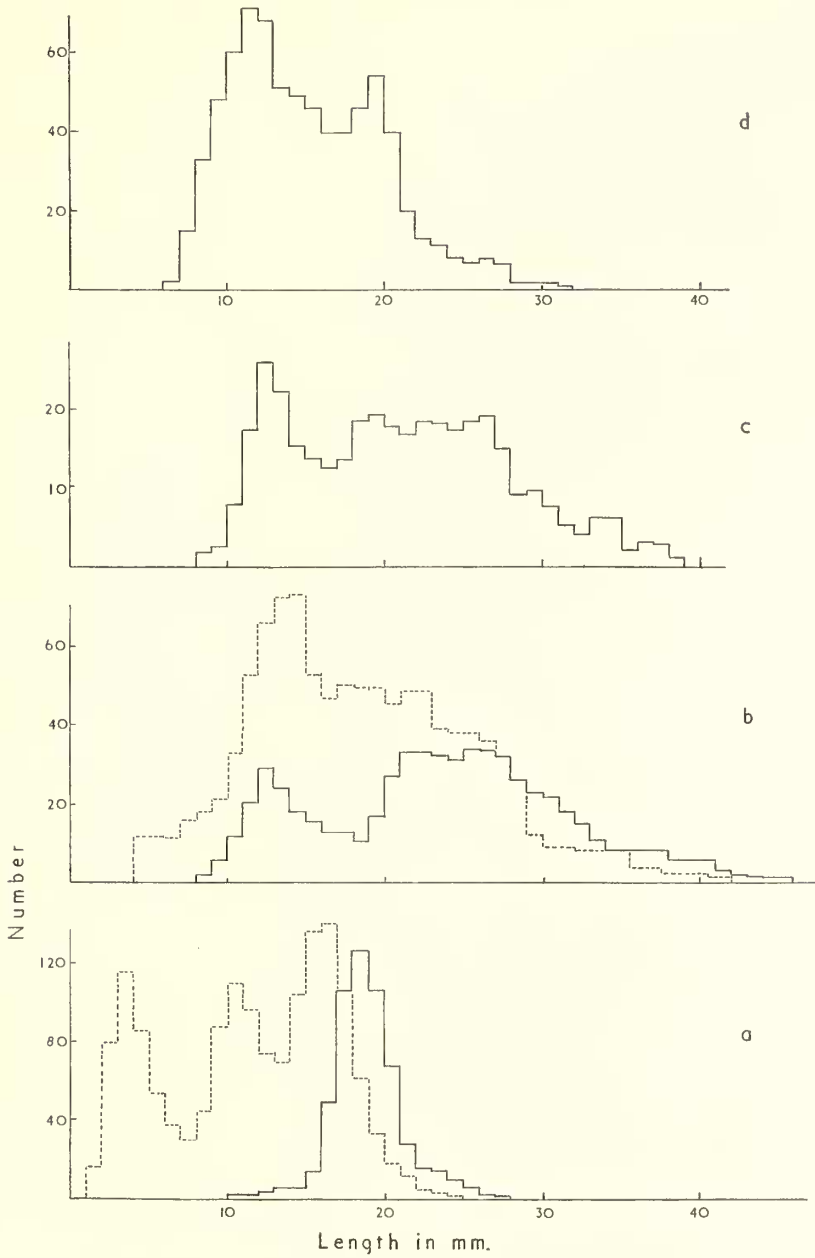
The size-frequency histogram (text-fig. 5*b*) of the articulated dead shells (10 per cent. of sample) shows three peaks, two of which (14.5 mm. and 21.5 mm.) can be related to the 1960 and 1961 winter rings of the living animals. The peaks appear to reflect increased mortality at times when conditions were severe and growth was negligible. The small peak at 34.5 mm. probably represents a few three-year old shells of pre-1960 vintage.

The right and left valves, forming 74 per cent. of the sample, were separated and measured. The size-frequency histograms of both valves were identical with modes at about 15 mm., and there had obviously been no preferential sorting of one valve as against the other. Accordingly, the histogram of the right valve only is shown (text-fig. 5*c*). The 15 mm. peak coincides almost exactly with the 1960 winter growth-ring of the living animals. Assuming that most of the valves belong to the 1960 generation, there is good evidence of high mortality during the winter of 1960 at a time when growth was at a minimum. On the other hand, the more severe winter of 1961 has resulted in a shell (i.e. articulated valve) peak rather than a valve peak. This may relate to the gradual rotting of the ligament of the dead shells of winter 1960 and their subsequent easy disarticulation during the winter storms of 1961.

By May 1962 most of the 1960 generation of cockles had died and the pattern of the resulting fossil population had been largely determined. If, on the other hand, the living animals had suddenly been killed at that date, the pattern of the total fossil assemblage (dead animals and shells + right valves representing former complete shells) would have been as shown in text-fig. 5*d*. There, a bimodal distribution is obvious. If the living animals, however, were to die gradually over the next year or so, the second peak would disappear and be replaced by a plateau, since growth in cockles after the second year is slight. Indeed, a sample of the 1960 cockle population taken in October 1962 showed that the mode had increased by only 2 millimetres over the May 1962 sample.

Description and interpretation of the Craigelaw Bay samples. A slightly different collecting procedure was adopted in this area. The living population was sampled and collections made of three valve assemblages from different parts of the beach.

Cockles were collected in April, May, and October 1962. The living animals of the April 1962 collection represent the spatfall of summer 1961. The size-frequency distribution (text-fig. 6*a*) is unimodal and very similar to that of the 1960 generation found in the Peffer Burn, except for the difference in modal size (18.5 mm. as opposed to 30.5 mm.). The growth-rings of the living animals fall into three distinct groups, one at 4.5 mm.



TEXT-FIG. 6. Size-frequency histograms of *Cardium edule* from Craigelaw Bay, East Lothian. Broken lines represent growth-ring size-frequencies. *a*, Living animals, April 1962. *b*, Valve assemblage from sand flat, May 1962. *c*, Valve assemblage from sand flat, October 1962. *d*, Valve assemblage from storm beach, May 1962.

(which like the Peffer examples must have formed shortly after settling), one at 10.5 mm., and the third at 16 mm. From our own observations and from Orton's data (1926), the 16 mm. ring appears to be the winter ring, whereas the 10.5 mm. ring is probably a disturbance ring caused by a unique rather than a seasonal event, an event, moreover, areally restricted, since it was not recorded by the cockles in the Peffer Burn about a mile eastwards of the bay.

Two recent valve assemblages—and as assemblages probably not more than six months old—were gathered in May 1962 from the bay area, one from the surface of the sand at the site of the earlier collection (text-fig. 6*b*) and the other from the storm beach at high-tide mark in the bay (text-fig. 6*d*). A further collection was taken from the sand flat in October 1962.

Although a period of five months had elapsed between collections from the bay flat, the size-frequency distribution of the two samples is markedly similar (text-fig. 6*b*, *c*) with a peak at 12.5 mm. and a plateau in the twenties. Summer tidal currents and storms had apparently had little effect on the size-frequency distribution pattern. The larger size of many of the valves precludes their derivation from the 1961 generation, and it is obvious that they belong to earlier generations now dead. The living generation therefore, unlike the Peffer collection, can have little bearing on the interpretation of the two valve assemblages.

Growth-ring analysis of the May valve assemblage (text-fig. 6*b*) reveals a strong peak at 14 mm., which is in good agreement with the valve peak at 12.5 mm. As in the Peffer cockles, the coincidence of growth-ring peaks and valve peaks is indicative of storm or winter conditions. The older year-classes of cockles tend to merge and become indistinct, and the positively skewed plateaux probably include two- and three-year olds. The small peak and plateau in the mid-thirties can be interpreted from hindsight as three-year olds, but we doubt if we would have recognized that group in an older valve assemblage where there were no living populations to help in identification.

The histogram (text-fig. 6*d*) of the storm beach collection reveals less variability than the bay flat collections some 50 yards distant. Small valves are more common and valves larger than 23 mm. are rare. The bimodal distribution compares closely with the growth-ring analysis of the 1961 generation, both in the coincidence of the disturbance ring with the 11.5 mm. valve peak and the living peak with the 19.5 mm. valve peak. We are not, however, arguing that the storm beach valves have been derived from the 1961 generation, rather that both samples appear to mirror conditions which have repeated themselves, i.e. that the valve peaks and growth-ring peaks are produced by seasonal conditions.

PALAEOECOLOGICAL SIGNIFICANCE

Growth-ring analysis. The conclusions in this section apply strictly only to populations of *Cardium edule*, but, because we believe that they are of more widespread application, we have phrased them in general terms. The limits within which the conclusions apply can be fairly clearly defined. They may be extended to bivalved animals with well-defined seasonal reproduction; growth-rings must be clear and preferably few in number. Infaunal species would appear to serve the purpose better than epifaunal ones, which tend to have more numerous growth-lines. Univalves (especially gastropods and ammo-

nites) with growth-lines could probably be analysed too, but with them the difficulties of measurement are generally much greater.

One of the unexpected results of the study has been the demonstration that disarticulated valves are essential to the ecological interpretation of a fossil population. Previous workers—ourselves included—have tended to ignore the valves, or at most used them as a means of indicating the energy level of the depositional environment. Yet the analyses clearly demonstrate that the disarticulated valves—the thanatocoenosis—are in some ways more important to palaeoecological interpretation than the fossil community. In a high-energy environment with unfavourable seasonal conditions, the fossil product is an abundant thanatocoenosis with strong size-frequency peaks. These peaks can be related to growth-rings produced by the survivors. In other words, those animals which were not killed by unfavourable conditions record those conditions as growth-rings.

It should be possible to determine whether polymodal peaks in fossil assemblages are purely the result of subsequent sorting so that certain sizes are selected, or whether they reflect events during the life of the parental population. Here again the coincidence of growth-ring peaks, and shell and valve peaks, would indicate events that occurred during the life of the population and not after death: a lack of correspondence would suggest subsequent sorting.

The average life-span of bivalves with well-marked seasonal rings has been determined by counting the number of estimated year-rings. This method has been used for living lamellibranchs (Kristensen 1959, Vogel 1959) and has been applied with some success to certain fossil brachiopods (Vogel 1959). It seems desirable to eliminate, so far as possible, subjective assessment of what is and what is not a winter (year) ring, for rings may be caused by a variety of events such as storms, salinity changes, excessive heat, sexual reproduction, &c. For this reason, we chose the more arduous method of recording every ring in the population sample and determined, from the resulting size-frequency plot, which sizes were the most significant. In this way, rings unique in the life of a few individuals become submerged in the dominant pattern. While it may be possible to judge which rings are winter rings in living species (cf. Mason 1959), we suggest that both methods should be used in determining the life span of a fossil species. It is especially difficult with either method to determine the significance of later growth-rings, since increments in adult shells tend to be small and variable, and therefore unreliable.

The discrimination of life and death assemblages. It is generally recognized that the first task of the invertebrate palaeoecologist is to distinguish fossil life and death assemblages by any means available. Boucot (1953), in an important contribution to the problem, suggested that the two types of assemblage should usually be distinguishable by means of size-frequency analysis. Life-assemblage histograms should characteristically have a strong positive skewness, with a sharp peak close to the origin, as a result of high juvenile mortality. Death-assemblage histograms, in contrast, should frequently approximate to bell-shaped normal distributions, because of size-sorting by currents and subsidiary factors. The two basic assumptions that Boucot makes in constructing his theoretical models warrant close scrutiny.

While it is true that invertebrates with an extremely high reproductive rate must have a high mortality in the youngest stages, it does not necessarily follow that this has direct

relevance to fossils, since this high mortality could be largely confined to the embryonic and larval stages which would not be preserved. There are virtually no reliable data on this type of organism (Deevey 1947) and there seems to be little justification at present for assuming as the general case that once benthonic organisms have settled successfully on the sea bottom they are appreciably more liable to die than adults. Such limited evidence as there is for mussels indicates rather the contrary. We have seen that the juvenile forms in the Ferny Ness community had a relatively low mortality during the period of study compared with the mature individuals. Savage (1956) kept some of the spat of the big Conway spawning in tanks, in conditions comparable with those in the natural environment, and found that mortality during a period of three years was negligible. There is some indication that the situation may not be different for other invertebrates.

A size-frequency study of a community of the brachiopod *Terebratella inconspicua* in New Zealand by Percival (1944) has been quoted as evidence that newly settled forms have a high mortality compared with the adults. A more thorough study by Rudwick (1962) has shown, however, that Percival's sample was atypical, probably as a consequence of selecting too small an area. Rudwick finds, in contrast to Percival, a high percentage of adults in his samples. Deevey (1947) quotes the results of a careful study of the settlement of the cyprid larvae of barnacles. Apparently the cyprids' chances of survival vary inversely with the density of attachment. When the density is low, most or all survive to become barnacles. The important point here is that, even when the mortality is high because of crowding, we are dealing with organisms that would not normally be preserved in the fossil state, and the survivorship curves for fully developed barnacles do not differ appreciably in character from those deduced for the Ferny Ness mussels (see below).

Obviously examples will be found where there has indeed been a high mortality during the first year of growth, as in the case of cockle population studied by Hancock and Simpson (1961); this would certainly have relevance to the fossil state. We merely wish to suggest that this is not necessarily the most common condition. It should be noted incidentally that Hancock and Simpson estimated mortality by measuring the density of the *living* cockles in a given area at different times, and did not record whether the organisms missing from their later samples were represented by empty shells (compare our results for the Peffer Burn cockles, which also suggest quite a high juvenile mortality).

We propose that the size-frequency distributions of benthonic invertebrate communities will frequently differ considerably from the simple models proposed by both Boucot (1953) and Olson (1957), and may actually be multimodal because of the significant representation of different age groups. This is evident in our study of both *Mytilus* and *Cardium*, and has also been demonstrated by one of us in the case of brachiopod life assemblages preserved more or less undisturbed in the Lias (Hallam 1961). The character of the distribution will depend primarily on three variables, growth-rate, mortality rate, and the annual recruitment of spat. Interaction between these variables will often give a complex distribution bearing little resemblance to a simple curve.

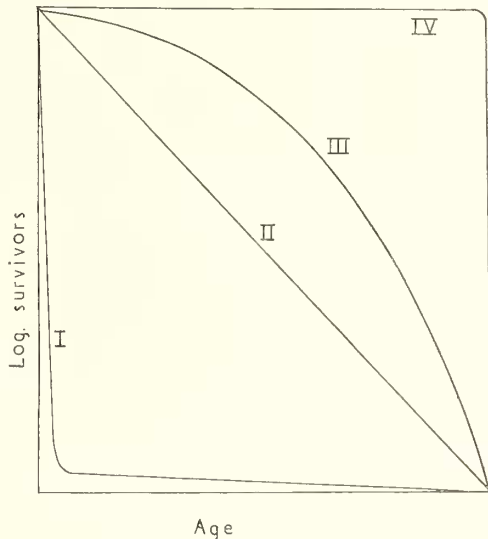
The second assumption we wish to contest is that the characteristically bell-shaped distribution of fossil death assemblages (Olson 1957) is largely the result of the selective removal of small shells by waves and currents, aided perhaps by their preferential solution during diagenesis owing to the greater surface area per volume exposed (though

this may be an important factor in the case of minute shells such as ostracods). Olson (1957) is impressed by the apparent anomaly between the size-frequency distributions of invertebrates deduced on theoretical grounds and those of most fossil assemblages.

It is clear, however, from the above discussion that undisturbed life assemblages may well approximate quite closely to symmetrical distributions in many cases. While, moreover, it is undeniable that currents are capable of transporting shells for some distance, as for instance when their competent velocity is less than that of the associated sediment (Menard and Boucot 1951), the evidence of both the *Mytilus* and sand flat *Cardium* valve assemblages cited in this paper suggests that this is not automatically to be assumed, even in high energy environments. Independent evidence is required, such as the elegant demonstration by Lever (1958) of the separation of lamellibranch valves of different hydrodynamic properties, and a good agreement in size distribution and the association of species of widely different mean size. An important distinction should be made between the disturbing action of oscillatory water movements (waves) within the environment of life, which may effect a high degree of disorientation and valve disarticulation, and powerful one-way currents capable of removing certain size grades of shells for a considerable distance into different environments.

Olson's recognition, from consideration of a large number of samples, that invertebrate death assemblages have a characteristically symmetrical size-frequency distribution is of considerable interest, since this is the geologically significant case. The relative rarity of small shells of a given organism cannot always be dismissed as collection failure, since it accords with the common experience even of palaeontologists who have looked carefully for such forms. Nor should diagenetic loss be invoked without independent evidence, except possibly in the case of minute shells. The results of our work demand the exploration of a further possibility, that many fossil death-assemblage distributions may largely reflect mortality.

Mortality rates, size, and age. Mortality rates in organisms can be expressed graphically by means of survivorship curves (Pearl 1940, Deevey 1947), in which the number of survivors is plotted on a logarithmic scale against age. Various types of curve are shown in text-fig. 7; cases I, II, and IV are discussed by Deevey (1947). Case I, the positively skew rectangular, signifies an extremely high mortality in the youngest stages. According to Deevey it has not yet been formally recognized in nature, but is presumed to be characteristic of marine species with pelagic larvae such as oysters, considering their



TEXT-FIG. 7. Theoretical cases of survivorship curve. I, Positive-skew rectangular—catastrophic juvenile mortality. II, Constant mortality. III, Constantly increasing mortality. IV, Negative-skew rectangular—catastrophic adult mortality following nearly 100 per cent. survivorship.

life span as a whole. Case II, the diagonal, signifies a constant mortality rate from birth, and is approximated after the fledgling stage by many species of birds. Case IV, the negatively skew rectangular, is characteristic of a cohort with a high incidence of survival which dies suddenly, and is probably only a laboratory curiosity. Deevey (1947) states that most reliably determined survivorship curves actually fall between cases II and IV. Accordingly, we have included a further curve in text-fig. 7 (case III). This has been calculated to signify a constantly increasing rate of mortality and must approximate a common condition in nature.

Data from the two important curves, cases II and III, have been plotted in terms of age-frequency (text-fig. 8*a, b*). Case II shows a strong positive skew, with the height of the curve increasing in constant proportion from the right. The position of the mode with respect to the origin will be determined by the class interval chosen. The finer the interval, the closer it will approach zero. Case III plots as a bell-shaped normal distribution.

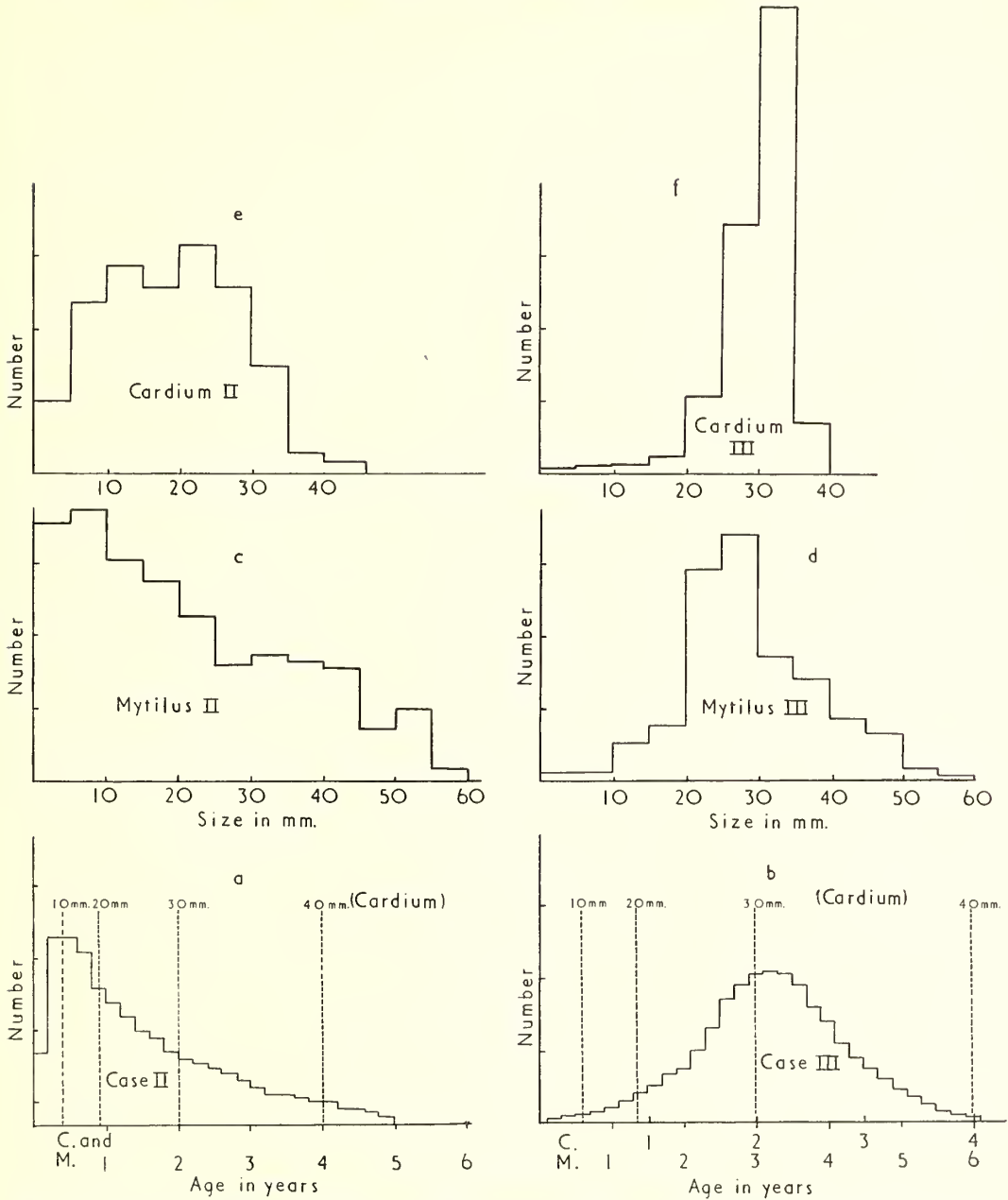
These results could be applied to fossils, whose age is not known, only if size increased linearly with age, which is rarely the case. To illustrate the sort of size-frequency distributions one may, in fact, expect we have taken data from the growth curves of *Mytilus* and *Cardium* illustrated in text-fig. 2 and replotted the age-frequency curves of text-fig. 8*a, b* as size-frequency histograms (text-fig. 8*c-f*). Because growth is rapid in the early years, animals dying during an early age interval tend to be spread through several size classes. Conversely, since growth is slow in the later stages of life, several age intervals of animals tend to be crowded within one size class.

The growth rate in *Mytilus* is the more constant, so that with a constant mortality rate the histogram (text-fig. 8*c*) retains its strong positive skewness. On the other hand, constantly increasing mortality rate is represented by a slightly positively skewed histogram (text-fig. 8*d*). The more rapidly changing growth-rate of Orton's cockles, however, results in a nearly symmetrical distribution with a constant mortality rate and a strongly negative skew with constantly increasing mortality rate (text-fig. 8*e, f*).

Size-frequency histograms of fossils do not therefore reflect *age* mortality rates, but indicate preserved deaths in each size class. Positively skewed distributions will normally tend to indicate something approaching constant mortality, while more symmetrical distributions may indicate either constant or increasing rates of mortality. To decide which, it is necessary to determine if possible the growth-rate by, for example, growth-ring analysis (cf. Vogel 1959).

An attempt has been made to construct approximate survivorship curves for our two *Mytilus* valve assemblages by determining the approximate age at a given size from Savage's data (text-fig. 9). It is assumed that slight variations in growth-rate between the Forth and the Conway will not materially affect the shape of the curves. There are a small number of large specimens above 65 mm. which fall significantly outside the normal distribution range of five year olds (text-fig. 3). These are, in consequence, treated as six year olds, and a few in the Craigelaw sample over 70 mm. as probably seven year olds. For the sake of simplicity and convenience, the only specimens considered are those whose size corresponds to the mean for complete years of growth. To facilitate comparisons it is usual to express the number of survivors as a percentage, but, as in this case the Craigelaw sample is approximately half the size of the Ferny Ness, numbers of the former have simply been doubled.

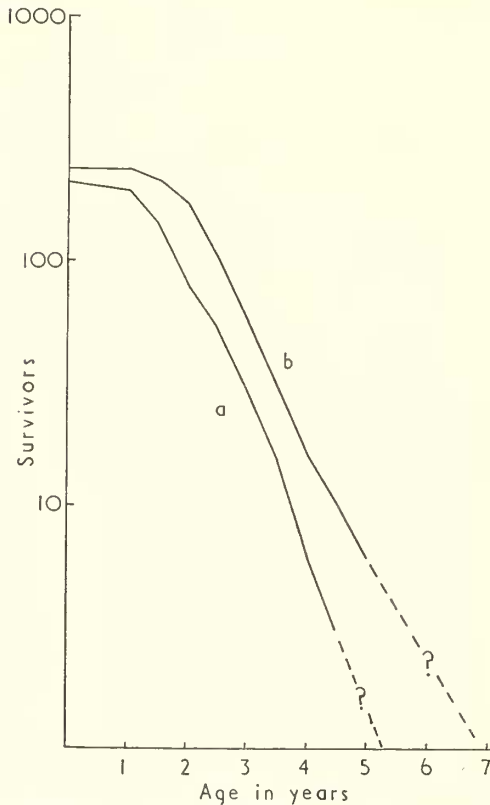
The two survivorship curves are closely similar and naturally apply only to the



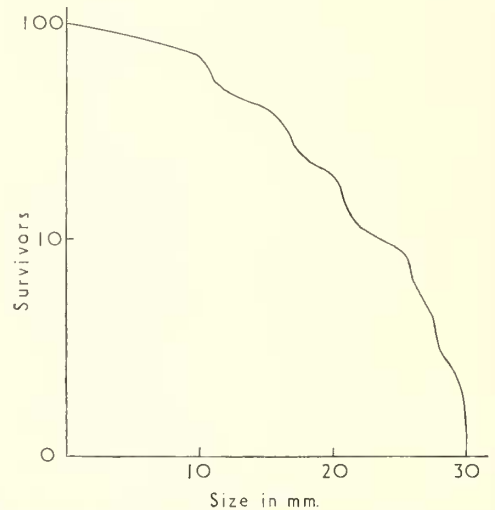
TEXT-FIG. 8. *a, b*, Theoretical age-frequency histograms for constant mortality (case II) and constantly increasing mortality (case III). *Mytilus edulis* (M.) and *Cardium edule* (C.) age scales where different are indicated. Data derived from text-fig. 7. *c, e*, Size-frequency histograms of constant mortality for *Mytilus edulis* and *Cardium edule* using data derived from text-fig. 2. *Cardium* 10 mm. age-size relationship plotted on *a* as example of technique used. 5 mm. intervals omitted for clarity. *d, f*, Size-frequency histograms of constantly increasing mortality for *Mytilus edulis* and *Cardium edule*. *Cardium* 10 mm. age-size relationship plotted on *b*.

successfully settled individuals. Both indicate a very low mortality rate up to the end of the first year, followed by a rapidly increasing rate during the second year, and the subsequent assumption of a fairly constant rate for the next two or three years. There is, finally, a suggestion of a slight decline in later years, rather more pronounced with the Craigelaw specimens.

A minor complicating factor in the study of mortality is that the rate may vary seasonally. To this seasonal change must be added the fact that increased mortality will



TEXT-FIG. 9. Survivorship curves of *Mytilus edulis* from storm beaches at Ferry Ness (*a*) and Craigelaw Bay (*b*), calculated from data of text-fig. 4 and Savage (1956).



TEXT-FIG. 10. Size-survivorship curve showing the effect of seasonal (annual) fluctuations in growth-rate of *Cardium edule* assuming constant mortality. Growth-data derived from Hancock and Simpson (1961).

often occur during the winter, when shell growth is at a minimum. Therefore, seasonal mortality changes may be magnified because animals, although dying over a period of months, die at the same size. This effect will show up as minor irregularities on the survivorship curve (text-fig. 10).

In conclusion, we suggest that the analysis of fossils in terms of survivorship is a potentially valuable tool for palaeoecologists, in providing indications of rates of mortality. But marine invertebrates which have obviously survived the high embryonic and

larval mortality may be susceptible to the type of mortality rates characteristic of higher animals, and the discovery of normal or slightly skewed size-distribution need not necessarily demand the invocation of other factors. The most promising assemblages for analysis are those embedded in fine-grained sediments, in which case the water movements must have been slight and shell solution restricted because of low permeability of the matrix. Size sorting can most safely be discounted when the assemblage includes species of appreciably different mean size.

Size-frequency histograms or polygons of death assemblages will normally be smoother than those of life assemblages, which may be multimodal because of the inclusion of different age groups. The case of the *Cardium* valve assemblage in Craigelaw Bay, with its clearly bimodal distribution, illustrates the situation that may arise if ultimate burial follows not long after the catastrophic killing of a young age group.

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APPENDIX

Incidence of Nucella predation on Mytilus. An interesting feature of the *Mytilus* shells in the Ferny Ness and Craigelaw thanatocoenoses is the presence of borings of the carnivorous gastropod *Nucella lapillus*, circular in shape and averaging 1 mm. in diameter.

Several things can be deduced from these borings. It is assumed that a boring right through the shell signifies a successful predation. Obviously only one valve needs to be penetrated and this has to be borne in mind in estimating the percentage of mussels that died through predation in an assemblage of disarticulated valves.

The percentage of successfully bored mussels is rather low, 6.4 per cent. in the Ferny Ness and 2.4 per cent. in the Craigelaw sample. The range in size of these mussels is 14 to 58 mm., with a mean of 35 mm. (closely similar in both samples). The gastropods seemed to have exerted little preference for any part of either valve, but it is noteworthy that in both samples the left valve was apparently preferred to the right, the number of borings differing by a factor of almost exactly two. This may relate to a preferred orientation of mussels in the living communities. There is some suggestion that the shell thickness exerts a controlling influence, certain of the large shells having one or more abortive or incomplete borings, with or without a successful boring where the thickness is less. One valve was observed, however, with a boring 4 mm. deep close to the umbo. This is far in excess of the average.

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